Article

Subfossils of extinct and extant species of Simuliidae (Diptera) from Austral and Cook Islands (Polynesia): anthropogenic extirpation of an aquatic insect?

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Abstract

Subfossil head capsules of Simuliidae larvae have been recovered from swamps on Tubuai and Raivavae of the Austral Islands, and Atiu and Mangaia of the southern Cook Islands. For Tubuai and Raivavae it is likely that the simuliids are extinct, but a single simuliid species is extant on nearby Rurutu. For Atiu and Mangaia, extant simuliids have not been reported, but are known on Rarotonga. Well-preserved head capsules indicate that the Cook Islands subfossils are those of *Simulium* (*Inseliellum*) *teruamanga* Craig and Craig, 1986. For the Austral Islands, the simuliid from Tubuai is considered a variant of *Simulium* (*Inseliellum*) *rurutuense* Craig and Joy, 2000. That from Raivavae is morphologically distinct and is described here as a new species, *Simulium* (*Inseliellum*) *raivavaense* Craig and Porch. Humans arrived in Eastern Polynesia *ca*. 1,000 years ago resulting in the widespread destruction of lowland forest and conversion of wetlands to agriculture with implied consequences for the indigenous biota of these habitats. Here we consider that one such result was loss of freshwater aquatic biodiversity.

Key words: Pacific, Polynesia, Cook Islands, Austral Islands, Simuliidae, *Simulium, Inseliellum*, larvae, subfossil, taxonomy, biogeography, extirpation, anthropogenic

Introduction

Fossils of Simuliidae date back to Late Jurassic (*ca*. 209 mya) (Currie and Grimaldi 2000; Grimaldi and Engel 2005, Borkent 2012), but those of larvae are extremely rare as flowing water is generally not conducive to fossilization. The best example of fossilized larvae are the remarkably detailed remains from the Koonwara Fossil Bed, Victoria, Australia (Jell and Duncan 1986). These Lower Cretaceous (*ca*. 138.5 mya) larvae are of the whole body and show most structures. They were preserved in a fine mudstone derived from a lake bottom—suggested by other preserved fauna. It was assumed that the simuliid larvae were swept there by a flood.

The material in this study is considered to be subfossil, that is, the remains are unmineralized. Similar material, in particular those of larval chironomid head capsules, are commonly encountered in lake sediments. There are few other examples of subfossil simuliid larval material, mainly from lake deposits in British Columbia; summarized by Currie and Walker (1992). That material consisted of ecdysed head capsules, some complete, but more usually just the ventral surface with the hypostomal teeth—still of considerable diagnostic utility. In Norway, Heiri (2004) used subfossil chironomid head capsules to compare faunal assemblage variability within lakes. Simuliid head capsules were recovered, but no further details were given, except that the capsules were accompanied by those of running water chironomids, indicating that they had been deposited from a stream or river.

The subfossils in this study are of simuliid larvae from sites in the Cook-Austral Islands, Central South Pacific Ocean (Fig. 1).

It is well known that Simuliidae are capable of trans-oceanic dispersal (Crosskey 1990, Craig *et al*. 2000, Adler *et al*. 2004, Craig *et al*. 2012 and others). Except for the Hawai'ian archipelago and the Falkland Islands, simuliids are known from most oceanic islands with running water—the habitat of the immature stages. Dispersal by Simuliidae has been examined in detail by Spironello and Brooks (2003) in relation to the MacArthur-Wilson

model of island biogeography, using details for Polynesian simuliids of subgenus *Inseliellum* (Craig *et al.* 2001). Their results were essentially in full agreement with the radiation zone hypothesis of MacArthur-Wilson, where larger islands (*e.g.* Tahiti) have more species than smaller islands, and islands further removed (*e.g.* Raiatea) from that source have more precinctive evolutionary events. In agreement with Craig *et al.* (2001) they concluded that movement of *Inseliellum* from the Cook Islands to the Austral Islands was <1 mya. In a different analysis, Adler *et al.* (2005) examined aspects of dispersal for simuliids on islands adjacent to the North American continent. They concluded that "the high frequency of precinctive species on islands 500 km or more from the nearest mainland indicates that at some distance beyond 100 km, open water provides a significant barrier to colonization and gene exchange".

The exact mechanism by which simuliids disperse long distances is unknown, but generally assumed to be via flight—probably wind assisted. Hocking's (1953) classic work on intrinsic flight distance of insects showed that unfed Nearctic simuliid females could fly 116 km in still air. However, Crosskey (1990) documents definitive dispersal examples of 300-500 km, and maybe further for African (Garms and Walsh 1988) and Canadian (Fredeen 1969) simuliids. Dispersal via birds cannot be ruled out, although there is no direct evidence for that (*e.g.*, Craig 2003a, Craig *et al.* 2003).

Distance is only one obstacle that simuliids face when dispersing and colonising; another is the size of the island. In his classic book "Islands", Menard (1987) explained that the size of an island and its position relative to the wind determines amount of rainfall and presence of running water—a necessity for simuliids. Smaller islands typically lack the elevation to generate clouds and substantive precipitation. Such islands merely receive the overall rainfall of the region. Another correlate for hot spot islands, such as the Society Islands, is that small size generally indicates older age and this aspect was examined in detail for the historical biogeography for *Inseliellum* by Craig and Currie (2001) and Craig (2003. His Fig. 2). In short, older islands of *ca.* 4 million years of age, being eroded and having subsided, even though still emergent, typically lack permanent running water and thus simuliids.

Yet, there are caveats to the above assertions. Position of island in relation to others can have major influence. Bora Bora of the Society Islands is downwind of Tahaa and Raiatea. Although small (22 km^2), Bora Bora has enough elevation (727 m) to capture storm clouds generated by turbulence (Xie *et al.* 2001) from the larger upwind islands. Thence, Bora Bora does have small streams and a black fly—*Simulium* (*Inseliellum*) *malardei* (Craig 1997). This species is wide spread in the Society Islands and considered phylogenetically basal and is a habitat generalist (Craig and Currie 1999, Craig 2003).
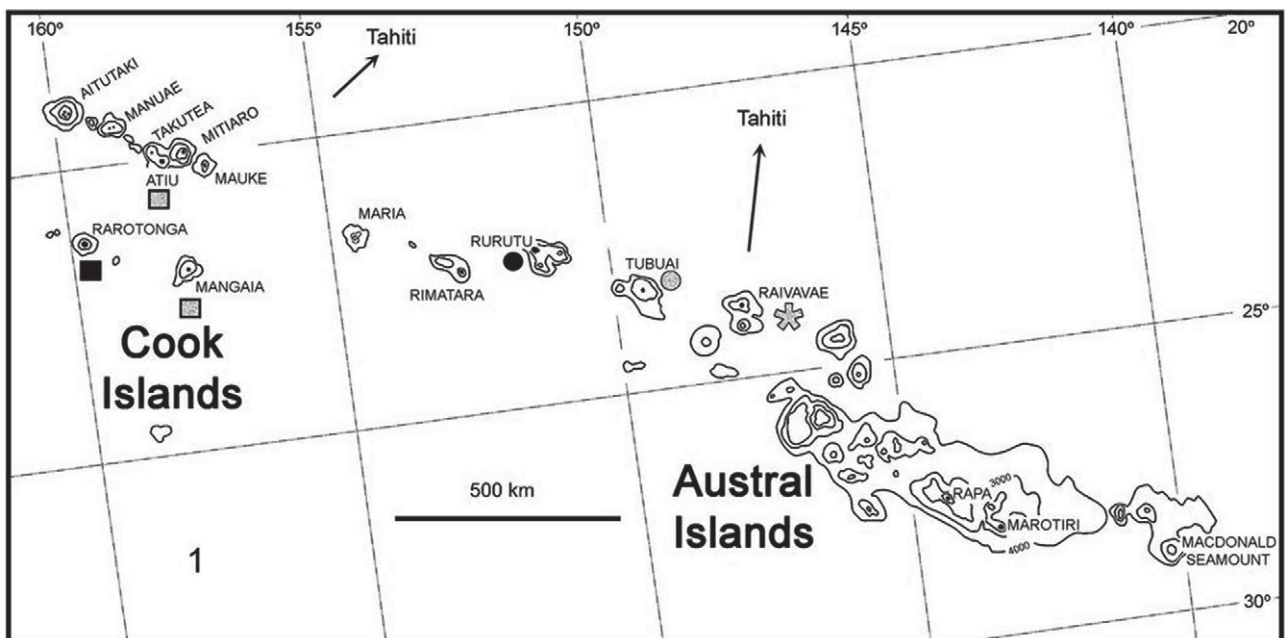

FIGURE 1. Distribution of known simuliid material on Cook and Austral Islands. *Simulium* (*I.*) *teruamanga*—squares, *S.* (*I.*) *rurutuense*—circles. *Simulium* (*I.*) *raivavaense*—asterisk. Solid shapes indicates extant species, stippled subfossil material. (Adapted from Craig *et al.* 2001).

The smallest island with an endemic species is Mohotani—one of the Marquesas Islands (Craig 2004). Fifteen kilometer directly south of Hiva Oa, with an area of just 12.2 km², and a gently sloping interior reaching only 520 m altitude, there is but a single stream of 400 m length; home to the endemic species *S. (I.) englundi*. The island has other precinctive flora and fauna (*e.g.*, Cibois *et al.* 2004).

The simuliids of Polynesia belong to the subgenus *Inseliellum*, a far flung taxon ranging from Micronesia, the Cook and Austral Islands, and into the Marquesas and Society Islands. The subgenus is related to that of *Nevermannia* in Australia and New Caledonia (Craig and Currie 1999). Within *Inseliellum* it is known (Rothfels *in* Craig 1983) that there are segregates which have distinct cytological arrangement of the nucleolar organizer. This characteristic was examined by Spironello (2002) and Spironello and Hunter (2005) who confirmed two clades based on the position of the nucelolar organizer, now named NO-IL and NO-IIL. *Simulium rurutuense* is a member of the NO-IIL segregate, which also includes species from the Marquesas Islands. This is consistent with morphological evidence (Craig and Currie 1999). Based on such characters, the subfossil material and the new species from Raivavae belong in the NO-IIL segregate.

The objectives of this paper are to identify new material and describe one new species. We update Craig *et al.*'s (2001) distribution patterns and biogeographic scenarios for simuliids, and paleogeology of the region. We also briefly discuss possible reasons for extinction or extirpation of simuliids on the islands; most likely through human intervention.

Material and methods

Subfossil head capsules were recovered from sediment cores from swamp sequences collected in 2008 (Austral) and 2009 (Cook). These cores were recovered using standard sampling techniques (D-Section or piston coring) and subsampled in the field into 5 cm (Raivavae, Atiu, Mangaia) or 10 cm (Tubuai) sections. Samples were returned to the laboratory where insects and plant macrofossil were recovered by washing the sediment with water through a 250 μm sieve and hand sorting the residues under a binocular microscope. Simuliids were picked from the insect residues and stored in 80% ethanol. The temporal sequence represented by each of the cores was determined by radiocarbon dating, details of which will be published elsewhere.

Simuliid material consisted of partial head capsules of larvae, including the hypostoma, postgenal cleft, genae and mandibular phragma (the cuticular bar supporting the mandible and antenna) (*e.g.*, Fig. 5, 7). Some specimens included the dorsal cephalic frontoclypeal apotome—and on one specimen, a single antenna (Fig. 7). The material is clearly moulted cuticle (exuviae) and embodies what we consider, based on size, to be mainly that from last larval instars, with a few from probable penultimate instars. As known from other Polynesian simuliid species, earlier instars show more plesiomorphic expression of the hypostomal teeth (Craig 1997).

We follow usage of terms for hypostoma suggested by Currie and Walker (1992) and Adler *et al*. (2004). There is a single median tooth, usually three sublateral teeth to either side, then a lateral tooth followed by variable numbers of paralateral teeth. Down the sloped sides of the hypostoma are a number of variously expressed serrations. There are a series of hypostomal setae (see sockets Fig. 4, 6, 11).

Arrangements of hypostomal teeth are an important diagnostic feature of *Inseliellum* larvae (Craig and Joy 2000 *e.g.*, their Figs. 32–43). The plesiomorphic condition of hypostomal teeth in *Inseliellum* is known from phylogenetic analysis (Craig and Currie 1999) and exemplified by the hypostoma of *S. (Inseliellum) malardei* that exhibits the common arrangement for *Simulium* in all larval instars, as noted above. Arrangements of hypostomal teeth in other *Inseliellum* species is known to be developmentally (ontogenetic) apomorphic. Earlier instar larvae exhibit the plesiomorphic condition with derived arrangements being expressed during the later instars (Craig 1997). For example, *S. oviceps* larvae where all the hypostomal teeth are subequally developed in later instars, show a distinct median tooth and lateral teeth in the first larval instar. This ontogenetic transformation can be partially seen here in the hypostoma of *S. raivavaense* n. sp., where the median tooth is better developed in the penultimate instar (*cf*. Fig. 16, 17).

Modification of the hypostoma includes multiplication of the sublateral teeth from three to four (*e.g.*, *S. teruamanga,* Fig. 4) and the paralateral teeth from one to up to six, with concomitant flattening and expansion. In the new species described here, the lateral serrations are more tooth-like (Fig. 16, 17).

Other pertinent diagnostic characters for larvae of *Inseliellum* species are the expression of cephalic cuticular corrugations, the number of head sensilla with raised bases, and pigmentation of the frontoclypeal apotome. Of lesser importance are the proportions of antennal articles (Craig and Joy 2000).

The subfossil head capsules were generally clean, so no treatment was applied except to manually remove larger pieces of dirt. While a hypostoma appears to be a single sheet of cuticle, it is actually double with a ventral and a dorsal surface. Debris trapped between the two layers cannot be removed. The cuticle was delicate and brittle, so the mountant of choice for microscope slides was polyvinyl lactophenol, which softens cuticle (Craig *et al*. 2012).

Images here were produced using a Wild M20™ compound microscope with a Nikon CoolPix 900™ digital camera. Stacks of images at different foci were combined using Helicon Focus™ and the resulting image manipulated in Photoshop Creative Suite™, following techniques used by Craig *et al*. (2012).

Description of species based on unique single specimens has been discussed previously by Craig (2004), who required that material exhibit one or more unique characters. This technique worked successfully for Polynesian simuliids where more specimens were eventually discovered, sometimes decades later. For other material, it was required that consistently recognizable material from multiple localities be available before specific status was accorded. Again, in retrospect, that approach was successful. We apply here the same reasoning to the subfossil material. Specimens from Raivavae are considered to be a new species, whereas the remainder not.

The holotype specimen of *Simulium* (*Inseliellum*) *raivavaense* Craig and Porch, has been deposited in the B. P. Bishop Museum, Honolulu, Hawai'i. Paratypes are also deposited there, as well as in the Australian National Insect Collection, CSIRO, Canberra, ACT, Australia. These types are on microscope slides. Other material still in alcohol is retained by the authors.

Geographic and geological aspects

The geological history of the Cook and Austral islands has been dealt with at a broad level by Dickinson (1998), Craig and Currie (2001), and Neall and Trewick (2008). In short, the islands are a series of 240 km wide, overlapping hot spot island chains that extend some 2,200 km from the almost-atoll Aitutaki in the Cook Islands, south-east through various other atolls and high islands to that of Rapa-iti and the Marotiri Rocks of the Austral Islands (Fig. 1). Recent detailed work by Bonneville *et al*. (2006) and others is summarized below.

The geological underpinnings of the Cook-Austral Islands is complex. The islands are emplaced on the so-called South Pacific Superswell, involved with a geochemically heterogeneous superplume of magma. The islands are known to be products of hot spot volcanoes, but understanding of the hot spots tracks has changed markedly over the last two decades. Only two hot spot tracks were recognized by Baudry *et al*. (1988), but three by Dupon (1993). Clouard and Bonneville (2001) addressed this problem of hot spots numbers on the Pacific Plate, giving times of origin and tracks of islands produced, including a Rurutu hotspot. Bonneville *et al*. (2006) using radiometric dating concluded that there are up to six hotspots, of which three appear to still be active, those of Rarotonga, Arago (Rurutu) and MacDonald.

The most linear of the hotspot island tracks arises from the Macdonald Seamount hot spot in the east and ends at Mangaia (age 19 my) in the southern Cook Islands. That age is consistent with distance from the hot spot and rate of movement of the Pacific Plate. The Northern Cook Islands, which are not considered here, are explained by a hotspot track that stopped producing magma at Raivavae at 6.5 mya. One island lineage, including nearby seamounts, and recognized as a hot spot track, extends from near Raivavae to Rurutu. Another extends from the recently named Arago Seamount, a hotspot southeast of Rurutu and terminates at Atiu of the Cook Islands (Bonneville *et al*. 2002). Rarotonga, previously puzzlingly youthful, now appears to have had its own hot spot which produced only that island (Clouard and Bonneville 2001), clarifying questions about its anomalous age, raised by Thompson *et al*. (1998).

Many of the islands under discussion here have a raised volcanic centre, but are surrounded by 'makatea' or uplifted fossil coral that has undergone weathering and dissolution. It is so named after the island Makatea of the Tuamotu islands, which is surrounded by spectacular cliffs of fossilized coral. The name refers to pure fresh water from caves in the coral. In the Cook Islands, Mauke, Mitiaro, Atiu and Mangaia are of this type and are often referred to as the 'makatea islands'. Stoddart *et al*. (1990) provide detailed geomorphology of the makatea Cook

Islands. Rurutu and Rimitara of the Austral Islands are also of this type. Clearly these islands have been submarine at some time and age of the makatea is important in determining how long simuliids may have been on the islands.

Observations and radiocarbon dating from coral reefs of Cook Islands by Woodroffe *et al*. (1990), show that there has been recent uplift of the islands within the Holocene (*i.*e., <11,000 ybp). On Mitiaro, however, coral has been dated at 34,000 ybp, but the majority is modern and of 3-5,000 years old, indicative of that recent uplift. Similarly for Atiu where marine benches and notches in the makatea too indicate Holocene uplift. Mangaia, the highest of the makatea islands, also has evidence of similar uplift. There is, though, evidence of older beach ridges up the central volcanic edifice, but none are dated (Stoddart *et al*. 1990). Rarotonga, on the other hand, shows little if any uplift. Indeed, with a small lagoon and coral reef it appears to be subsiding; typical of hot spot islands that have moved off the magma plume (Craig 2003). Reasons for the uplift of the Cook makatea islands is moot, but is generally considered to be caused by the loading of Rarotonga on the lithosphere and consequent upward warping in a ring around the island (Stoddart *et al*. 1990, Dickinson 1998, Thompson *et al*. 1998). If that is so, then the makatea islands have been above sea level less than the age of Rarotonga—1.5 mya. This is an important date to establish since it determines the maximum time these islands could be colonized by simuliids.

Craig *et al*. (2001, His Table 1) incorrectly indicated that there was no running water on Atiu and Mangaia. He did, however, note that these islands were probably implicated in dispersal of *Inseliellum* into French Polynesia.

Observations and description

Cook Islands. Rarotonga has rainfall in the order of 3,500 mm annually and there are numerous permanent streams. Two simuliids species are known; one, *Simulium* (*Inseliellum*) *teruamanga* is common in most streams. An enigmatic species, *S*. (*I.*) *matavera,* Craig and Craig is known only from one locality and then from limited material. It has not been found since, but is, on the basis of its karyotype and morphology of the pupal exuviae, related to the Society Island simuliids, not the Cook-Austral Islands segregate (Craig and Craig 1986).

There is nothing that distinguishes the Atiu subfossils from extant material of *S. teruamanga* from Rarotonga. Of importance is that one specimen from Atiu has the frontoclypeal apotome and the basal articles of an antenna still attached (Fig. 7). The colour pattern of the apotome, still evident, matches closely that of extant *S. teruamanga* (Fig. 2). The antenna, too, has the same length proportions of basal and median articles as seen in that species (Craig and Craig 1986). More definitively, the hypostomal teeth arrangement (Fig. 8) barely differs from that of *S. teruamanga* (Fig. 4) and any divergences fall well within known variation of that of *S. teruamanga*. We therefore deem the material from Atiu to be that of *S. teruamanga.*

Topographical maps of Atiu show drainage patterns, but no water courses as such. Rainfall is in the order of 1,970 mm annually. Flowing water is known to exist on the island at times, but not during dry years when El Niño climatic patterns predominate (Gerald McCormack, pers. comm. 2010). There are, however, at least two permanent freshwater springs that supply the swamps. Both springs are currently badly perturbed by domestic pigs, and the probability that they support extant populations of simuliids is low; however, neither stream has actually been prospected. The subfossil material is derived from a core taken by Prebble, Wilmshurst and Porch in 2009, approximately 50 metres from Lake Te Roto (S20.00833º W158.12278º), at an elevation of about 8 metres. Simuliid subfossils are restricted to the lower, mainly prehuman part of the core below depths of 125 cm and date to before 1300 AD.

Nothing distinguishes subfossils recovered on Mangaia from extant populations of *S. teruamanga* from Rarotonga or Atiu. However, only the ventral surface of head capsules have been recovered so far (Fig. 5). The slightly broader expression of the hypostomal teeth and variation in number (3–4) of the sublateral teeth (Fig. 6) fall within known variation of those of *S. teruamanga*. Hence, we consider the material from Mangaia to be that of *S. teruamanga.*

Mangaia has permanent water courses emptying into swamps. The probability of extant simuliid residents is high, although the island has not been surveyed. Craig and Craig (1986) previously commented that simuliids were likely to occur there.

Subfossil head capsules are derived from a core collected in 2009 by Prebble, Wilmshurst and Porch, from near the outlet of the Tamarua East swamp. They are infrequently represented in the core, but in contrast to records from other islands continue to close to the surface. This suggests the possibility that simuliids may still be extant on the island.

Austral Islands. The westernmost inhabited Austral island, Rimatara (Fig. 1) is 216 km east of the atoll Maria, the most westerly land of the Austral Islands. The island consists of a circular volcanic plateau with the highest altitude of 95 m at Mount Uhau. The plateau has rolling terrain with definite drainage patterns. Although smaller, it is remarkably similar to Mangaia of the Cook Islands with its makatea-bounded swamps. However, the drainages typically lack running water and no subfossil simuliids were recovered from any of several sedimentary sequences collected by Prebble and Porch in 2008. However, subfossils of mosquito larval heads that appear to be *Culex annulirostris* Skuse (Ralph Harback, pers. comm. 2010) have been recovered. This taxon is known to be extant in the Austral Islands and Rimatara (Huang 1977) and widely distributed across the western Pacific (Belkin 1962). A sample of these *Culex* specimens is deposited in the Strickland Museum, University of Alberta (UASM).

Age of origin for Rimatara is confusing. Craig *et al*. (2001) give dates ranging from 25-5 mya, but Bonneville *et al*. (2006) with better recent dating cite 27 mya. How long the island has been above sea level is not known. Has Rimatara at some time had simuliids, precursors to those on islands to the east?

Rurutu has small streams that flow over smooth eroded basalt and which support a single simuliid, *Simulium (Inseliellum) rurutuense* Craig and Joy. Larvae of this simuliid occur in astronomical numbers on vegetation in fast flow. Craig (2003) noted that the aquatic fauna of the island was depauperate. Englund (2004), on the other hand, in a detailed examination of running water on Rurutu, found ephydrid, tipulid, and ceratopogonid flies, as well as crustaceans.

Simulium rurutuense has distinctive larvae, in particular the colour pattern on the larval frontoclypeal apotome (Fig. 9). It can be further distinguished from *S. teruamanga* of Rarotonga on the basis of more developed cuticular corrugations and raised bases to sensilla on the head (Craig and Joy 2000). Karyological examination by Spironello and Hunter (2005) revealed that *S. rurutuense* is a member of the NO-IIL clade, along with *S. teruamanga* (Rarotonga), *S. buissoni* and *S. hukaense* (Marquesas).
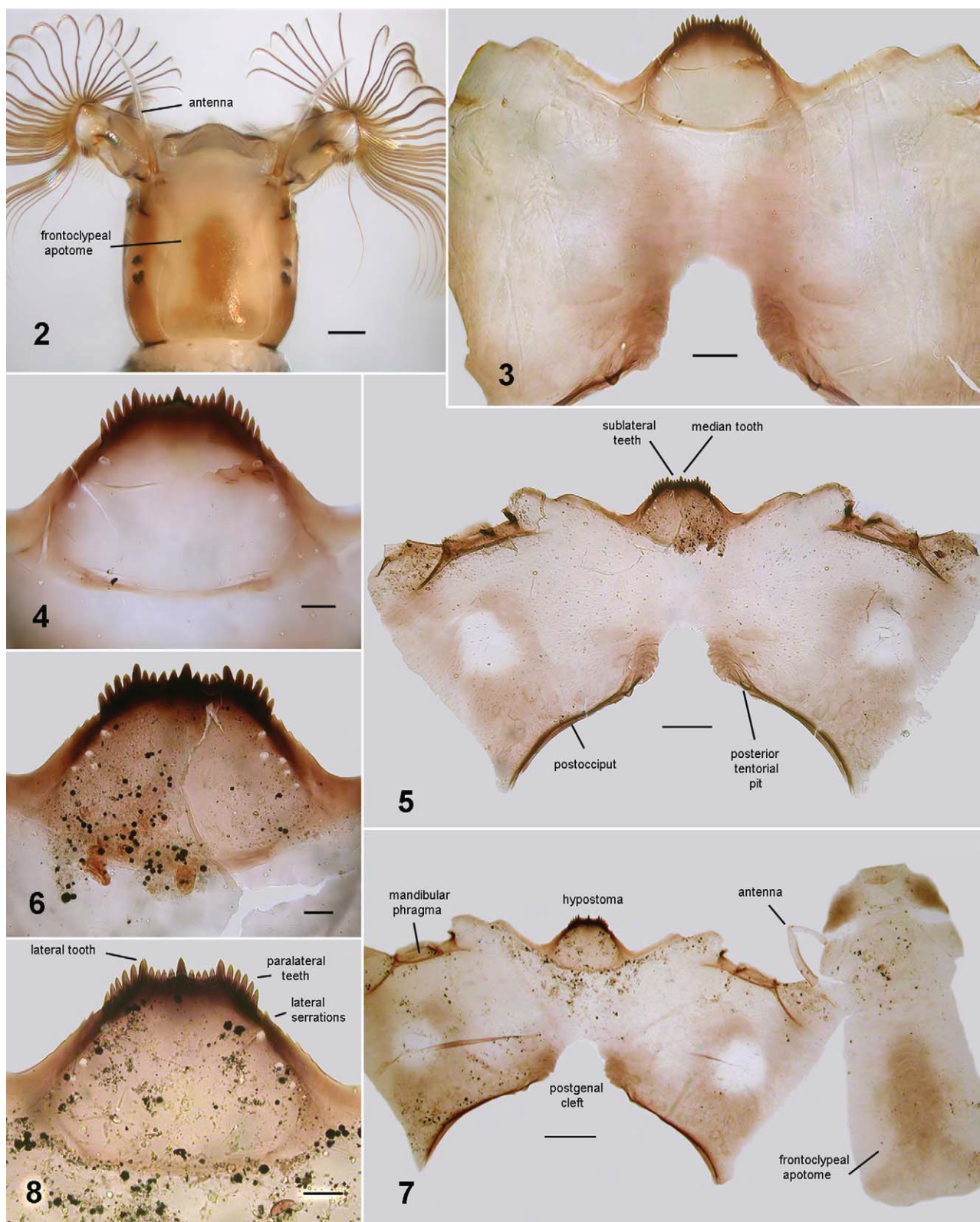
Rurutu has a complex geologic history. Its raised central area is surrounded by makatea, indicative of uplift that in this instance involved renewed volcanicity. Recent basalt actually intermixes through the makatea. Thence, ages given for Rurutu are dichronic (Chauvel *et al*. 1997). The shield building phase was *ca*. 12.3 mya and the later volcanicity occurred at *ca*. 1.1 mya (Bonneville *et al*. 2006). Reconnaissance examination of Rurutu low areas by Porch in 2008 revealed no sites with extended organic sediment sequences—subfossil simuliids are therefore unknown for Rurutu.

Tubuai is 213 km SE of Rurutu and although a small island its topography is, in places, steep. There is an extensive lagoon and coral reef with small islands or *motu*. Chavel *et al*. (1997) show dates of formation for Tubuai ranging from 12.2-8.8 mya. Bonneville (2005) gives an average age of 9.2 mya. The island does not appear to have been completely submerged at any time, as indicated by lack of makatea. Watersheds are relatively small and radiate out from Mount Panee (alt. 392 m) and Mount Taitaa (alt. 422 m), flowing out into large swampy areas, such as the 'Marais Matavahi'.
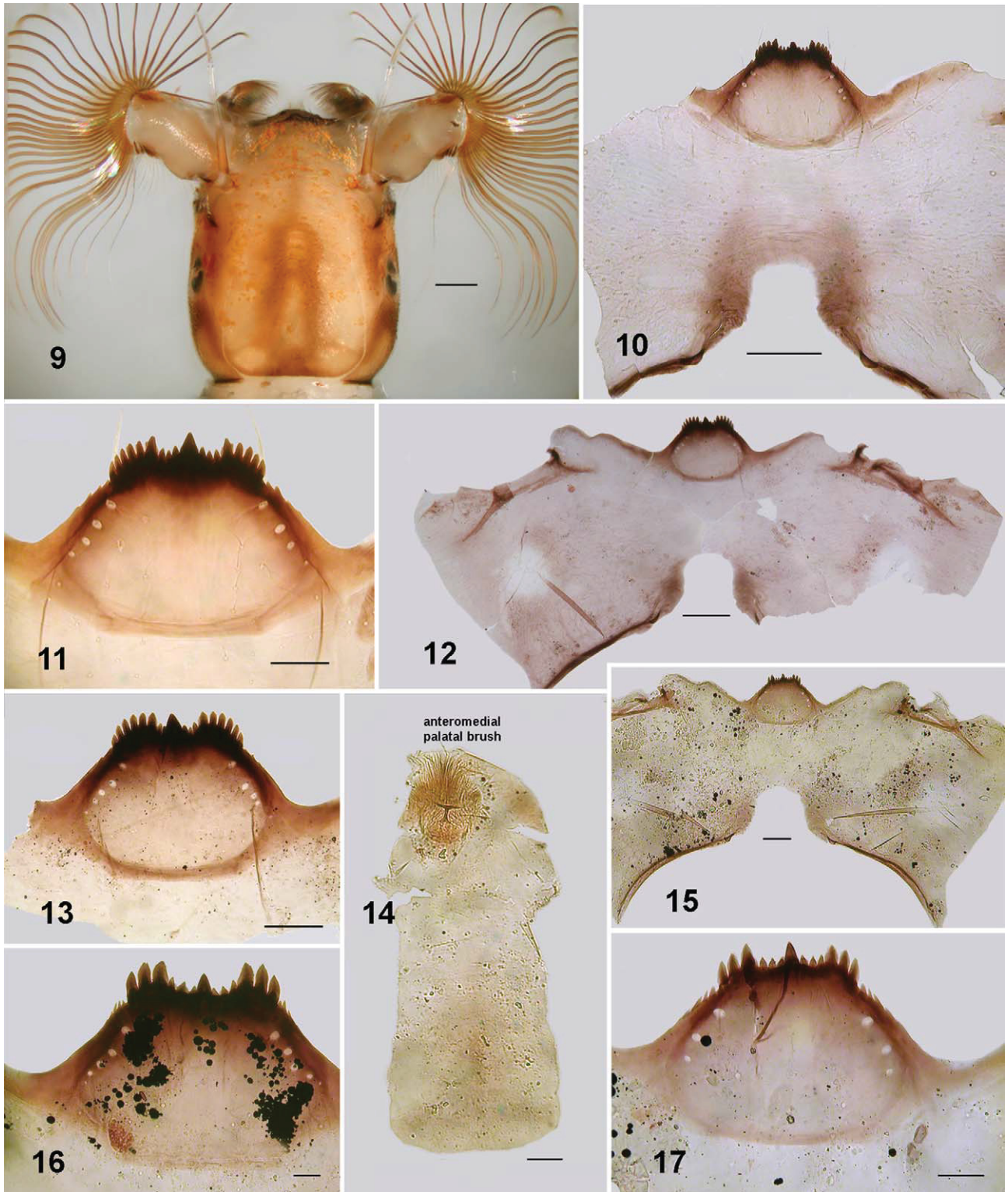
Sampling of streams by Englund (2004) was not extensive. Streams have densely shaded lower reaches, with substrate generally of cobble. At higher elevations there were chutes and plunge pools. This contradicts Craig (2003) who did not see the streams at higher altitude. Further, Englund found considerable diversity of aquatic insects not noted by Craig (2003).

Extant simuliids were not found by either Craig or Englund. Subfossil simuliids, however, have been recovered from Mihiura Swamp, in the southwest of the island (S23.38222º W149.49778º alt. 18 m). Here a 4.3 metre peat sequence collected by Prebble and Porch in 2008 has revealed simuliids to be restricted to depths of >2.7 metres: no simuliids are known from the post-human arrival period after *ca*. 1300 AD. Material consisted of the ventral head capsule and none had the frontoclypeal apotome. The hypostoma, while showing (Fig. 13) slightly deviant morphology (smaller sublateral teeth) from those of the extant *S. rurutuense,* were not considered to be sufficiently different (*cf*. Fig. 11) to designate a new species. All subfossils from Tubuai were considered to belong to *S. rurutuense.*

Raivavae is 191 km east of Tubuai and is the largest of the Austral Islands. Of steep topography it rises to 437 m at Mount Hiro. There is a narrow fringe of flat fertile land; swamps are not extensive, but do occur. Never completely submerged, Raivavae has been dated at 6.5 mya and is considered part of a volcanic chain extending from there to Rurutu Island including seamounts (dated at 12 mya) forming the 'Raivavae hot spot track' (Bonneville *et al*. 2006).

FIGURES 2–8. *Simulium* (*I.*) *teruamanga*. Fig. 2. Dorsal view of head of extant larva. Matavera Stream, Rarotonga (scale bar 0.1 mm). Fig. 3. Hypostoma and postgenal cleft of extant larva (scale bar 0.05 mm). Fig. 4. Hypostoma of extant larva (scale bar 0.02 mm). Fig. 5. Hypostoma, postgenal cleft and genae of subfossil larva. Near outlet Tamarua East swamp, Mangaia (scale bar 0.1 mm). Fig. 6. Hypostoma of subfossil larva. Near outlet Tamarua East swamp, Mangaia (scale bar 0.02 mm). Fig. 7. Hypostoma, postgenal cleft, frontoclypeal apotome and antenna of subfossil larva. Near Lake Te Roto, Atiu (scale bar 0.1 mm). Fig. 8. Hypostoma of subfossil larva. Near Lake Te Roto, Atiu (scale bar 0.02 mm).

FIGURES 9–17. 9–13. *Simulium* (*I.*) *rurutuense*. Fig. 9. Dorsal view of head of extant larva. Vaipapa Stream, Rurutu (scale bar 0.1 mm). Fig. 10. Hypostoma and postgenal cleft of extant larva (scale bar 0.1 mm). Fig. 11. Hypostoma of extant larva (scale bar 0.02 mm). Fig. 12. Hypostoma, postgenal cleft and genae of subfossil larva. Mihiura Swamp, Tubuai (scale bar 0.1 mm). Fig. 13. Hypostoma of subfossil larva (scale bar 0.05 mm). **14–17**. *Simulium* (I.) *raivavaense*. Near Rairua, Raivavae. Fig. 14. Frontoclypeal apotome of extinct subfossil larva—note anteromedial palatal brush (scale bar 0.05 mm). Fig.15. Hypostoma, postgenal cleft and genae of extinct subfossil larva (scale bar 0.05 mm). Fig. 16. Hypostoma of last instar of extinct subfossil larva (scale bar 0.02 mm). Fig. 17. Hypostoma of probable penultimate instar of larva (scale bar 0.02 mm).

Englund's (2003) examination of the aquatic fauna of Raivavae showed short drainages similar to those of Rurutu. Although supporting a variety of habitats, the island lacks introduced fish and the ubiqitous neritid snails of the Central Pacific. Also absent were commonly encountered taxa on other islands including simuliids, dolichopodids and saldids. Odonates, on the other hand, were present.

Subfossil simuliids are present in a sedimentary sequence collected in a swamp near Rairua at approximately 2-3 metres above sea-level (S23.86851° W147.67853°). In this dominantly organic sequence, simuliids are restricted to depths of greater than 1.5 metres and like Tubuai, in sediments predating the arrival of humans. The subfossil material from Raivavae shows marked differences in development of the hypostomal teeth and colour pattern of the frontoclypeal apotome from those of *S. rurutuense*. We therefore consider the Raivavae subfossil simuliid to be a new species.

***Simulium* (*Inseliellum*) *raivavaense* Craig and Porch, sp. nov.**
Figures: 14–17

Diagnosis. Larva: hypostoma with three sublateral teeth, lateral tooth and two paralateral teeth broadly flattened and slightly recurved medially. Frontoclypeal apotome with pigmentation not in figure eight configuration. Postgenal cleft U-shaped.

Description (Based on holotype, paratypes and numerous other specimens).

Adults. Unknown.

Pupa. Unknown.

Larva. Last instar. Head capsule: moderately pigmented, the postocciput and hypostoma more so (Fig. 15). Frontoclypeal apotome (Fig. 14): cuticle corrugated with bases of sensilla raised, neither markedly so; with darker medial and posterior pigmentation, similar to that of *S. teruamanga* (Fig. 2, 7), markedly different from that of *S. rurutuense* (Fig. 9); ecdysial line not sinuous, sharply rounded posterolaterally (Fig. 14). Hypostoma (Fig. 16): median tooth distinct, apex markedly posterior to line of lateral teeth; three sublateral teeth small and flanged; lateral tooth and two paralateral teeth markedly prominent, flattened and slightly recurved medially; serrations three to five, small, sharp. Five hypostomal sensilla. Postgenal cleft U-shaped, smoothly rounded apically (Fig. 14). Posterior tentorial pits not markedly developed, albeit distinct. Mandibular phragma not markedly extended ventrally.

Probable penultimate instar. Hypostoma (Fig. 17). Median tooth prominent, sublateral teeth of equal length, lateral tooth and paralateral teeth as for last instar; serrations three, as for last instar. Three hypostomal sensilla.

Type data. **Holotype**: Microscope slide, ventral head capsule of larva. Label details:-*"Simulium/* (*Inseliellum*)/ *raivavaense*/ Austral Islands/ Raivavae, nr. Rairua/ S23.86851 W147.67853/ Acq. #17239 BPBM/ PVLP D. A. Craig. 2010/ HOLOTYPE (red)"*. Deposited Bernice P. Bishop Museum, Honolulu, Hawai'i.

Paratypes—four. As for holotype, but with PARATYPE. One probable penultimate instar with frontoclypeal apotome deposited Bernice P. Bishop Museum, Honolulu. Three, one of penultimate instar, deposited Australian National Insect Collection (ANIC), CSIRO, Canberra, Australia.

Material examined. Holotype, paratypes, numerous other specimens.

Distribution (Fig. 1). Austral Islands, Raivavae.

Etymology. Named for the Austral Island, Raivavae.

Remarks. Recognizing a species of simuliid merely on the basis of incomplete subfossil larval head capsules is problematic. However, the hypostomata are well preserved, including one frontoclypeal apotome, and provide clear evidence about the specific distinctiveness of this material. Using the hypostoma as a major diagnostic character for species has been successfully employed by Craig and Joy (2000) for Polynesian simuliids and the overall problem was discussed by Craig (1987, 1997). *Simulium raivavaense* differs markedly in hypostomal expression from that of extant *S. rurutuense* from Rurutu (Fig. 3, 4) and subfossil material from Tubuai. The median and sublateral teeth are relatively similar in size, but the lateral and paralateral teeth differ—*S. rurutuense* has five to six paralateral teeth, whereas there are only two markedly enlarged such teeth in *S. raivavaense*. In *S. rurutuense* the median tooth is subequal in length to the most prominent lateral teeth (Fig. 11), whereas in *S. raivavaense* the median tooth is markedly shorter (Fig. 16). The serrations also differ distinctly—small and rounded in *S. rurutuense*, sharp and distinct in *S. raivavaense*.

There is little question that *S. raivavaense* falls within the Cook-Austral Islands clade of species (*S. teruamanga* plus *S. rurutuense*), agreeing in expression of hypostomal teeth, cuticular corrugation and raised sensilla bases. That this is probably the correct grouping is confirmed by the poorly developed ventral extension of the mandibular phragma in *S. raivavaense*. This character state is expressed in the majority of *Inseliellum* species, but not a small segregate of Society Islands species, the *mesodontium* -subgroup, which have superficially similar hypostoma.

Simulium raivavaense and *S. rurutuense* can be distinguished from *S. teruamanga* by possession of only three sublateral teeth on either side of the median tooth of the hypostoma; the latter species has four.

Subfossil simuliid material from Raivavae included a single specimen that retained the frontoclypeal apotome and shows specific differences from *S. rurutuense*. The apotome has a pigmentation pattern (Fig. 14), albeit faint, more like that of *S. teruamanga* (Fig. 2), not the figure-of-eight shape diagnostic for *S. rurutuense* (Fig. 9). Further the hypostomal teeth have only two paralateral teeth and the serrations are developed as small teeth, not rounded structures as for *S. rurutuense*. The median tooth is poorly developed (*cf*. Fig. 11, 16). That this is a derived condition is bolstered by the more generalized development of the teeth in a penultimate instar subfossil (Fig. 17) where the median tooth is more prominent. Such ontogenetic development of apomorphic hypostomal teeth is well known for *Inseliellum* (Craig 1997).

The site of collection of this material is today an extensively weed-invaded former taro swamp: immediately adjacent to the core site there are extensive contemporary taro gardens. Prior to human arrival (sometime not long before 1300AD) the sediments suggest significantly more running water and a forested landscape paralleling the general trends in other palaeo-records from the region (Anderson and Kennett 2012).

Rapa-iti, often referred to as Rapa, further to the east lacks introduced fish and crustaceans (Englund 2004). Simuliids are not known from this island, neither are subfossils, so an assumption might be that they never reached this far east. Rapa appears to have less biogeographic affinity to the other Austral Islands than it does to the Society Islands (Englund 2004; Gillespie *et al*. 2008). A sedimentary sequence from Rapa (Core 2 of Prebble *et al*. 2012) has been examined for insect remains and despite containing extensive subfossil insect material, none are of simuliids.

Discussion

Biogeographic Implications

Discovery of *Inseliellum* subfossil larval head capsules is a valuable addition to the extensive understanding of this simuliid subgenus in the Pacific. In particular it provides information that allows a more detailed biogeography to be proposed for these simuliids in the Cook-Austral islands.

The subfossil material clearly can be assigned, on morphological evidence, to the Cook-Austral Islands clade of *Inseliellum*, sister to the lineage of Marquesas *Inseliellum* (Craig and Currie 1999, Craig *et al*. 2001). Craig (1983) was first to offer comments about biogeography of Polynesian simuliids, but given the state of knowledge at that time he placed little confidence in the proposed scenario. Simuliids were not known from the Austral Islands at that time, but he did suggest they had entered the Cook Islands via Rarotonga and Mangaia (the latter for which simuliids were then not known) some 1.8-1.2 mya. Subsequent biogeographic analyses have not substantially changed that original scenario. Craig *et al*. (2001) postulated entry of *Inseliellum* into Polynesia less than 20 mya via the Cook Islands, with dispersal of the NO-IIL clade north to the Marquesas Islands at 6 mya and into the Austral Islands at 1 mya. That scenario was based largely on the then known ages of islands. A further detailed examination by Spironello and Brooks (2003), using the radiation zone hypothesis of the MacArthur-Wilson theory of island biogeography, agreed in full with the Craig *et al*. (2001) hypothesis. Gillespie *et al*. (2008), in a major review of French Polynesian faunal biogeography was also in general agreement. However, they used more modern ages for islands (Clouard and Bonneville 2005) and biogeographic scenarios of older mien for other Austral Island fauna were proposed.

Given the subfossil simuliid material, we suggest below two distinct scenarios, one for the Cook Islands and one for the Austral Islands.

If it is assumed that the source of the Cook Island simuliids (*S. teruamanga*) is Rarotonga and that the recent

uplift of the makatea islands of Atiu and Mangaia (and the others of Mitiaro and Mauke) was the result of lithosphere flexure by the weight of Rarotonga during its formation, then the current subaerial phase of these islands cannot be older than Rarotonga, that is 2.3-1.6 mya. Indeed, probably considerably less since lithosphere flexing would take time as the size and weight of Rarotonga increased. Dating of Cook Island makatea (Woodroffe *et al*. 1990, Stoddart *et al*. 1990) indicates that considerable uplift of these islands occurred during the Holocene, that is, less than 11,500 ybp and some even more recent, in the order of 5,000 ybp—little time for evolutionary divergence. But there are older uranium-based Pleistocene ages for coral on Mauke of 38,570-31,150 ybp, and for Mitiaro 34,050-32,780 ybp, with the majority of ages of 36,200-5,140 ybp (Woodroffe *et al*. 1990).

The small distances between islands (*e.g*., a maximum of 220 km between Rarotonga and Atiu)—little more than the known active flight range for some simuliids (*e.g*., Hocking 1953), provides good congruence with MacArthur and Wilson's classic hypothesis of island biogeography regarding distance from source.

Divergence times for simuliid speciation has been suggested for the Society Island species *Simulium dussertorum* and *S. oviceps*. Joy *et al*. (2007) showed that time to most recent common ancestor for *S. oviceps* was 1.77 my, that for a cascade ecotype 1.70 my and for a river ecotype 0.89 my. They noted that the latter age is close to the time the central caldera of Tahiti-nui collapsed producing the catchment area of the large Papanoo River, preferred habitat for the river ecotype. *Simulium dussertorum* also has two such ecotypes and appears to be divergent from *S. oviceps* at 1.05 my. There are detectable morphometric differences in larval body size and labral fan dimensions between the two ecotypes. Craig (1987) originally considered *S. dussertorum* to be merely an ecological variant of *S. oviceps*, later recognizing it as a separate species (Craig 1997). That action was substantiated by Joy and Conn (2001) using molecular data. Even so, the two species are not particularly easy to distinguish morphologically. In short, one million years produced minor morphological divergence in those lineages.

It is tempting to apply the times of molecular divergence vis-a-vis morphological divergence for *S. oviceps* and *S. dussertorum* against the subfossils from the Cook-Austral Islands. We do so, albeit superficially, bearing in mind that 'molecular clocks' develop at heterogeneous rates across taxonomic groups and are local, not universal (Avise 2004). On that latter point we are also mindful that the Cook-Austral Island simuliids are in a distinct clade (Spironello and Hunter 2005) from those of the Society Island and from which those divergence dates were derived (Joy and Conn 2001). Nonetheless, precinctive evolution of simuliids in Polynesia has taken place on islands very close to the species source, for example *S. englundi* on Mohotani, some 20 km south of Hiva Oa, Marquesas Islands. The islands of Rarotonga, Atiu and Mangaia are all within possible flight range of adults of *S. teruamanga*. Of equal importance is present above sea-level existence of the latter pair of islands—less than 1.5 mya and with recent Holocene uplift (Woodroffe *et al*. 1990). Earlier orogeny has little relevance here since the islands were submarine. If one applies the molecular and morphological divergence rates from Tahitian *S. oviceps* and *S. dussertorum*, of *ca*. 1.0 my for minor body size and labral fan differences, it is clear that the almost total lack of morphological divergence in the hypostomal teeth and pigmentation of the frontoclypeal apotome (Fig. 4, 6, 7, 8) between simuliids of the three islands (Rarotonga, Atiu and Mangaia) is to be expected, because of insufficient time. Accordingly we consider the subfossils from Atiu and Mangaia to be of *S. teruamanga*.

For the simuliids of the Austral Islands a scenario proposed by Garb and Gillespie (2006) and Gillespie *et al*. (2008) for thomisid crab spiders might be applied, but with caveats—for example, they have markedly different dispersal methods and habitat requirements. The spiders on Rurutu and Tubuai are more closely related to each other than they are to those from Raivavae and Rapa and it was suggested that, for the first two older islands, colonization might have been between 7.9-4.9 ma and colonization of the latter two younger islands at about 3.8-2.5 ma. In other words, there was a stepwise colonization from older to younger islands—west to east. The genetic evidence for Raivavae and Rapa is, however, not as clear-cut as that for the older islands. Their scenario ignores the evidence (makatea and two ages of basalt) that Rurutu has been submerged and only recently become subaerial some 1.8-1.0 mya. Hence, a refinement of Gillespie's model might involve origin of the spiders on Tubuai with back dispersal to Rurutu (2-1 mya) and thence to the younger easterly islands. Another possibility is that that the islands of Maria (13.8 mya) and Rimatara (14.0 mya), now small and of low relief, could have been involved. But as noted by Bonneville (2005) ages for these islands are unreliable. A conundrum for the spiders is that Rurutu, with a recent age younger than Tubuai, has a spider clade that is phylogenetically basal to some lineages on Tubuai.

Morphologically the simuliid subfossils from Tubuai (Fig. 12, 13) barely differ from those of extant populations on Rurutu (Fig. 10, 11); thus we consider that material to be *S. rurutuense*. If the rate of divergence

known for the Society Island *Inseliellum* applies (Joy *et al.* 2007) this indicates less than 1 mya separation, in agreement with the time Rurutu has been above sea level. For the present, we suggest that *Inseliellum* initially colonized the Austral Islands via Tubuai, with back dispersal to Rurutu.

The subfossils from Raivavae are sufficiently morphologically distinct that they constitute a new species—*Simulium* (*Inseliellum*) *raivavaense*. The same reasoning as described above indicates that the divergence time has been greater than 1 mya. Accordingly, colonization of Raivavae from Tubuai may have been well before that to Rurutu.

Human Driven Extirpations?

A major question regarding the Cook-Austral Islands simuliids is why they disappeared from some islands. As noted by Craig (2003), there comes a time in the eventual demise of a hot spot island when it cannot sustain a running water fauna, though it takes some millions of years for erosion and subduction to produce an uninhabitable (for simuliids) island. Similar suggestions have now been incorporated in a new model of island biogeography for volcanic islands (see Whittaker *et al.* 2008, 2009). All the islands under consideration still have running water, with Raivavae, in particular, having several permanent streams. On the other islands potential habitats for simuliids are still present (or at least were present in the very recent past). The extirpations and extinctions revealed here, however, cannot be explained by geological history, largely because these disappearances occurred too recently and coincided with the transformation of the insular biota as a consequence of the arrival of people.

How could humans alter the aquatic habitats of these islands to cause extirpations, or perhaps even the extinction of *S. raivavaense*? One possible explanation is that this species, and indeed *S. teruamanga* on Atiu and Mangaia, are still present on their respective islands, though so decreased in abundance that they have eluded detection by collectors. Given the extensive surveys for aquatic insects that have been undertaken on both Tubuai and Raivavae we are of the opinion that this scenario is less likely than that for human-induced extirpation/extinction.

It is well known that the arrival of prehistoric humans had devastating consequences for the biodiversity of Pacific islands (Cowie 2001; Steadman 2006; Prebble and Dowe 2008). The processes that drove these extinctions include forest clearance, burning, and the introduction of non-native species. Forest clearance and replacement of lowland swamp forests with anthropogenic fern/sedge swamp habitats and agricultural systems, burning and extensive erosion would have altered the hydrology of these small island systems (Prebble and Wilmshurst 2009). Given that the hydrological settings of these islands were presumably already on the edge of suitability for simuliids, any major alteration of hydrology that increased sediment loads, nutrients and decreased oxygenation would contribute to an increased likelihood of extirpation or extinction. These extirpations are a potentially worrying sign in regard to the maintenance of aquatic biodiversity on islands and elsewhere on the planet in the face of increasing rates of human modification to ecosystems and extinction of insect species (Dunn 2005).

References

Adler, P.H., Currie, D.C. & Wood, D.M. (2004) *The Black Flies (Simuliidae) of North America*. Cornell University Press, New York, 941 pp.

Adler, P.H., Giberson, D.J. & Purcell, L.A. (2005) Insular black files (Diptera: Simuliidae) of North America: tests of colonization hypotheses. *Journal of Biogeography*, 32, 211–220.
http://dx.doi.org/10.1111/j.1365-2699.2004.01156.x

Anderson, A. & Kennett, D.J. (2012) Taking the high ground: the archeology of Rapa, a fortified island in remote east Polynesia. *Terra Australis*, 37, 1–288.

Avise, J.C. (2004) *Molecular markers, natural history, and evolution*. 2nd Edition. Sinauer Associates, Massachusetts, 684 pp.

Baudry, N., Von Stackelberg, U. & Recy, J. (1988) *Comptes Rendu de l'Academie des Sciences (SII) – Paris*, 306, 643–648.

Belkin, J.N. (1962) *Mosquitoes of the Pacific*. Vols.1 & 2. University of California Press, California. 608 pp.

Bonneville, A., Le Sauvé, R., Audin, L., Clourard, V., Dosso, L., Gillot, P.Y., Janey, P., Jordahl, K. & Maamaatuaiahutapu, K. (2002) Arago Seamount: The missing hotspot found in the Austral Islands. *Geology*, 30, 1023–1026.
http://dx.doi.org/10.1130/0091-7613(2002)030%3C1023:ASTMHF%3E2.0.CO;2

Bonneville, A., Dosso, L. & Hildenbrand, A. (2006) Temporal evolution and geochemical variability of the South Pacific superplume activity. *Earth and Planetary Science Letters*, 244, 251–269.
http://dx.doi.org/10.1016/j.epsl.2005.12.037

Borkent, A. (2012) The pupae of Culicomorpha—morphology and a new phylogenetic tree. *Zootaxa*, 3396, 1–98.

Chauvel, C., McDonough, W., Guille, G., Maury, R. & Duncan, R. (1997) Contrasting old and young volcanism in the Rurutu Island, Austral chain. *Chemical Geology*, 139, 125–143.
http://dx.doi.org/10.1016/S0009-2541(97)00029-6

Cibois, A., Thibault, J.-C. & Pasquet, E. (2004) Biogeography of eastern Polynesian Monarchs (Pomarea): an endemic genus close to extinction. *The Condor*, 106, 837–851.
http://dx.doi.org/10.1650/7491

Clouard, V. & Bonneville, A. (2001) How many Pacific hotspots are fed by deep-mantle plumes? *Geology*, 29, 695–698.

Clouard, V. & Bonneville, A. (2005) Ages of seamounts, islands and plateau on the Pacific plate. *Geological Society of America Special Papers*, 388, 71–90.

Cowie, R.H. (2001) Invertebrate invasions on Pacific islands and the replacement of unique native faunas: a synthesis of the land and freshwater snails. *Biological Invasions*, 3, 119–136.

Craig, D.A. (1983) Phylogenetic problems in Polynesian Simuliidae (Diptera: Culicomorpha): a progress report. *GeoJournal*, 7, 533–541.
http://dx.doi.org/10.1007/BF00218527

Craig, D.A. (1987) A taxonomic account of the black flies (Diptera: Simuliidae) of the Society Islands-Tahiti, Moorea and Raiatea. *Quaestiones Entomologicae*, 23, 372–429.

Craig, D.A. (1997) A taxonomic revision of the Pacific black fly subgenus *Inseliellum* (Diptera: Simuliidae). *Canadian Journal of Zoology*, 75, 855–904.
http://dx.doi.org/10.1139/z97-108

Craig, D.A. (2003) Geomorphology, development of running water habitats and evolution of black flies on Polynesian islands. *BioScience*, 53, 1079–1093.
http://dx.doi.org/10.1641/0006-3568(2003)053[1079:GDORWH]2.0.CO;2

Craig, D.A. (2003a) Deconstructing Gondwana—words of warning from the Crozet Island Simuliidae (Diptera). *Cimbebasia*, 19, 157–164.

Craig, D.A. (2004) Three new species of *Inseliellum* (Diptera: Simuliidae) from Polynesia. *Zootaxa*, 450, 1–18.

Craig, D.A. & Currie, D.C. (1999) Phylogeny of the Western-Central Pacific subgenus *Inseliellum* (Diptera: Simuliidae). *Canadian Journal of Zoology*, 77, 610–623.

Craig, D.A. & Craig, R.E.G. (1986) Simuliidae (Diptera: Culicomorpha) of Rarotonga, Cook Islands, South Pacific. *New Zealand Journal of Zoology*, 13, 357–366.
http://dx.doi.org/10.1080/03014223.1986.10422669

Craig, D.A. & Joy, D.A. (2000) New species and redescriptions in the Central-Western Pacific subgenus *Inseliellum* (Diptera: Simuliidae). *Annals of the Entomological Society of America*, 93, 1236–1262.
http://dx.doi.org/10.1603/0013-8746(2000)093[1236:nsarit]2.0.co;2

Craig, D.A., Currie, D.C. & Joy, D.A. (2001) Geographical history of the central-western Pacific black fly subgenus *Inseliellum* (Diptera: Simuliidae: *Simulium*) based on a reconstructed phylogeny of the species, hot-spot archipelagoes, and hydrological considerations. *Journal of Biogeography*, 28, 1101–1128.
http://dx.doi.org/10.1046/j.1365-2699.2001.00619.x

Craig, D.A., Currie, D.C. & Vernon, P. (2003) *Crozetia* Davies (Diptera: Simuliidae): redescription of *Cr. crozetensis*, *Cr. seguyi*, number of larval instars, phylogenetic relationships and historical biogeography. *Zootaxa*, 256, 1–39.

Craig, D.A., Craig, R.E.G. & Crosby, T.K. (2012) Simuliidae (Insecta: Diptera). *Fauna of New Zealand*, 68, 1–336. Crosskey, R.W. (1990) *Natural history of blackflies*. John Wiley & Sons, New York. 711 pp.

Currie, D.C. & Grimaldi, D. (2000) A new black fly (Diptera: Simuliidae) genus from mid Cretaceous (Turonian) amber of New Jersey. *In*: Grimaldi, D. (Ed.), *Studies on fossil amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, pp. 473–485.

Currie, D.C. & Walker, I.R. (1992) Recognition and paleohydrologic significance of fossil black fly larvae, with key to the Nearctic genera (Diptera: Simuliidae) *Journal of Paleolimnology*, 7, 37–54.
http://dx.doi.org/10.1007/BF00197030

Dickinson, W.R. (1998) Geomorphology and geodynamics of the Cook-Austral Island-Seamount Chain, in the South Pacific Ocean; implications for hotspots and plumes. *International Geology Review*, 40, 1039–1075. http://dx.doi.org/10.1080/00206819809465254

Dunn, R.R. (2005) Modern insect extinctions, the neglected majority. *Conservation Biology*, 19, 1030–1036. http://dx.doi.org/10.1111/j.1523-1739.2005.00078.x

Englund, R.A. (2003) Report for the 2002 Pacific Biological Survey, Bishop Museum Austral Islands, French Polynesia expedition to Raivavae and Rapa iti. *Pacific Biological Survey, Contribution No.* 2003-004, 1–30.

Englund, R.A. (2004) Report for the 2003 Pacific Biological Survey, Bishop Museum Austral Islands, French Polynesia expedition to Tubuai and Rurutu. *Pacific Biological Survey, Contribution No.* 2004-001, 1–29.

Fredeen, F.J.H. (1969) Outbreaks of the black fly *Simulium arcticum* Malloch in Alberta. *Quaestiones Entomologicae*, 5, 341–372.

Garb, J.E. & Gillespie, R.G. (2006) Island hopping across the central Pacific: mitochondrial DNA detects sequential colonization of the Austral Islands by crab spiders (Araneae: Thomisidae). *Journal of Biogeography*, 33, 201–220. http://dx.doi.org/10.1111/j.1365-2699.2005.01398.x

Garms, R. & Walsh. J.F. (1988) The migration and dispersal of black flies: *Simulium damnosum* s.l., the main vector of human onchocerciasis. *In*: Kim, K.C. & Merritt ,R.W. (Eds.), *Black flies: ecology, population management, and annotated world list*. Pennsylvania State University, University Park, pp. 201–214.

Gillespie, R.G., Claridge, E.M. & Goodacre, S.L. (2008) Biogeography of the fauna of French Polynesia: diversification within and between a series of hot spot archipelagos. *Philosophical Transactions of the Royal Society Biological Sciences*, 363, 3335–3346. http://dx.doi.org/10.1098/rstb.2008.0124

Grimaldi, D. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, New York, 755 pp.

Heiri, O. (2004) Within-lake variability of subfossil chironomid assemblages in shallow Norwegian lakes. *Journal of Paleolimnology*, 32, 67–84. http://dx.doi.org/10.1023/B:JOPL.0000025289.30038.e9

Hocking, B. (1953) On the intrinsic range and speed of flight of insects. *Transactions of the Royal Entomological Society of London*, 104, 223–345.

Huang, Y.-M. (1977) The mosquitoes of Polynesia with a pictorial key to some species associated with filariasis and/or dengue fever. *Mosquito Systematics*, 9, 289–322.

Jell, P.A. & Duncan, P.M. (1986) Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwara Fossil Bed (Korumburra Group), South Gippsland, Victoria. *In*: Jell, P.A. & Roberts, J. (Eds.), *Plants and invertebrates from the Lower Cretaceous Koonwarra Fossil bed, South Gippsland, Victoria*. Association of Australasian Palaeontologists, Sydney, pp 111–205.

Joy, D.A. & Conn, J.E. (2001) Molecular and morphological phylogenetic analysis of an insular radiation in Pacific black flies (*Simulium*). *Systematic Biology*, 50, 18–38.

Joy, D.A., Craig, D.A. & Conn, J.E. (2007) Genetic variation tracks ecological segregation in populations of Pacific island black flies. *Hereditary*, 99, 452–459.

Menard, H.W. (1987) *Islands*. Scientific American Library Inc., New York. 230 pp.

Neall, V.E. & Trewick, S.A. (2008) The age and origin of the Pacific Islands: a geological overview. *Philosophical Transactions of the Royal Society*, B. 363, 3293–3308.

Dupon (1993) *Atlas de la Polynésie Française*. Éditions de l'ORSTOM. ORSTOM, Paris, 113 pp.

Prebble, M., Anderson, A. & Kennett, D.J. (2012) Forest clearance and agricultural expansion on Rapa, Austral Archipelago, French Polynesia. *The Holocene*, 23, 179–196. http://dx.doi.org/10.1177/0959683612455551

Prebble, M. & Dowe, J.L. (2008) The late Quaternary decline and extinction of palms on oceanic Pacific islands. *Quaternary Science Reviews*, 27, 2546–2567. http://dx.doi.org/10.1016/j.quascirev.2008.09.015

Prebble, M. & Wilmshurst, J.M. (2009) Detecting the initial impact of humans and introduced species on island environments in remote Oceania using palaeoecology. *Biological Invasions*, 11, 1,529–1,556. http://dx.doi.org/10.1007/s10530-008-9405-0

Spironello, M. (2002) *A cytophylogenetic study of Pacific black flies (Diptera: Simuliidae)*. M. Sc. Thesis, Brock University, St. Catherines, Ontario. 119 pp.

Spironello, M. & Brooks, D.R. (2003) Dispersal and diversification: macroevolutionary implications of the MacArthur-Wilson model, illustrated by *Simulium* (*Inseliellum*) Rubstov (Diptera: Simuliidae). *Journal of Biogeography*, 30, 156–1573. http://dx.doi.org/10.1046/j.1365-2699.2003.00945.x

Spironello, M. & Hunter, F.F. (2005) Polytene chromosomes of an archipelagic subgenus, *Inseliellum* (Diptera: Simuliidae). *Genetica*, 123, 217–226. http://dx.doi.org/10.1007/s10709-004-2282-2

Steadman, D.W. (2006) *Extinction and Biogeography of Tropical Pacific Birds*. University of Chicago Press, Chicago, 594 pp.

Stoddart, D.R., Woodroffe, C.D. & Spencer, T. (1990) Mauke, Mitiaro, and Atiu: geomorphology of makatea islands in the Southern Cooks. *Atoll Research Bulletin*, 341, 1–65. http://dx.doi.org/10.5479/si.00775630.341.1

Thompson, G.M., Malpas, J. & Smith, I.E.M. (1998) Volcanic geology of Rarotonga, southern Pacific Ocean. *New Zealand Journal of Geology and Geophysics*, 41, 95–104.
http://dx.doi.org/10.1080/00288306.1998.9514793

Whittaker, R.J., Triantis, K.A. & Ladle, R.L. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, 35, 977–994.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2009) A general dynamic theory of oceanic island biogeography: extending the MacArthur-Wilson theory to accommodate the rise and fall of volcanic islands. *In*: Losos, J.B. & Ricklefs, R.E. (Eds.), *The theory of Island Biogeography revisited*. Princeton University Press, pp. 88–115.

Woodroffe, C.D., Stoddart, D.R., Spencer, T., Scoffin, T.P. & Tudhope, A.W. (1990) Holocene emergence in the Cook Islands, South Pacific. *Coral Reefs*, 9, 31–39.
http://dx.doi.org/10.1007/BF00686719

Xie, S.-P., Liu, W.T., Liu, Q. & Nonaka, M. (2001) Far-reaching effects of the Hawaiian Islands on the Pacific Ocean-atmosphere system. *Science*, 292, 2057–2060.
http://dx.doi.org/10.1126/science.1059781